ECOGRAPHY

Research

The role of extreme rain events in driving tree growth across a continental-scale climatic range in Australia

Alison J. O'Donnell, Michael Renton, Kathryn J. Allen and Pauline F. Grierson

A. J. O'Donnell (https://orcid.org/0000-0001-7597-7965) ✉ (alison.odonnell@uwa.edu.au), M. Renton and P. F. Grierson, School of Biological Sciences, The Univ. of Western Australia, Perth, Western Australia, Australia. MR also at: School of Agriculture and Environment, The Univ. of Western Australia, Perth, Western Australia, Australia. – K. J. Allen, School of Ecosystem and Forest Sciences, The Univ. of Melbourne, Richmond, Victoria, Australia; and, ARC Centre of Excellence in Australian Biodiversity and Heritage, Univ. of New South Wales, Sydney, New South Wales, Australia.

Ecography
44: 1–12, 2021
doi: 10.1111/ecog.05671

Subject Editor: Kenneth Feeley
Editor-in-Chief: Miguel Araújo
Accepted 5 April 2021

Rainfall regimes in many parts of the world have become increasingly dominated by fewer, but more extreme, rainfall events. Understanding how tree growth responds to changes in the frequency and intensity of rain events is critical to predicting how climate change will impact on forests and woodlands in the future. In this study, we used five tree-ring records of the native Australian conifer *Callitris columellaris* that span a large (> 20°) latitudinal and climatic gradient from the mesic (tropical) north to the xeric (semi-arid) south of Australia to investigate how inter-annual and spatial variation in the delivery of rainfall (the intensity and frequency of rain events) influences tree growth. In semi-arid biomes (~300–400 mm rainfall annually), tree growth is most strongly related to the amount of rainfall from heavy (> 75th percentile) rain days or the number of extreme (> 90th percentile) rain days, regardless of differences in the seasonal distribution and average intensity of rainfall among sites. Our findings also indicate that there is likely a minimum threshold amount of daily rainfall (~5 mm) that is required to stimulate tree growth in the semi-arid zone. In contrast, in the tropics (> 800 mm annual rainfall), inter-annual variation in growth is best explained by total growing season rainfall or the number of rain days > ~5 mm (~50th percentile of rain days) rather than extreme rainfall. Our findings indicate that not all rain events are important for driving tree growth, which has important implications for interpreting climatic signals in tree rings. Our findings also indicate that projected increases in the intensity of extreme rain events are likely to have contrasting impacts on tree growth across biomes, with greater and positive impacts on growth in semi-arid biomes and potentially negative impacts on growth in tropical biomes of Australia.

Keywords: *Callitris*, dendroclimatology, precipitation, rainfall intensity and frequency, ring width, thresholds, tree growth, tree rings

NORDIC SOCIETY OIKOS

www.ecography.org

Introduction

Extremes of rainfall are potentially more important drivers of plant processes than mean conditions (Knapp et al. 2002, 2008, Kulmatiski and Beard 2013, Reyer et al. 2013, Zeppel et al. 2014). Consequently, shifts in the frequency or intensity of extreme rain events are likely to have significant impacts on plant processes, ecosystem productivity and carbon dynamics (Reyer et al. 2013). However, despite pervasive observations and projections of increases in the frequency and intensity of extreme rainfall events in many regions of the world (IPCC 2013, Alexander 2015, Monier and Gao 2015, Donat et al. 2016, Good et al. 2016, Mallakpour and Villarini 2017, Myhre et al. 2019), remarkably little is known of how important extreme rain events are for driving plant processes, particularly the growth of woody plants, and thus how plant growth may respond to changes in the frequency and intensity of extreme rain events.

The importance of extreme rain events for driving ecosystem productivity and woody plant growth likely differs among biomes depending on their typical potential evapotranspiration and rainfall rates (Reynolds et al. 2004, Gerten et al. 2008, Knapp et al. 2008, Kulmatiski and Beard 2013, Guan et al. 2014, Zeppel et al. 2014, Manea and Leishman 2018). Extreme rain events are thought to be particularly important for driving woody plant growth in xeric (i.e. arid and semi-arid) biomes, where rain events are typically small (< 5 mm) and a large fraction of rainfall is lost to evaporation before it can infiltrate the soil profile (i.e. potential evapotranspiration exceeds rainfall by > 2.5 times; Knapp et al. 2008, Raz-Yaseef et al. 2012). Extreme rain events can infiltrate deeper into the soil profile and result in proportionately smaller evaporative losses than smaller rain events in xeric biomes (Kulmatiski and Beard 2013, Tugwell-Wootton et al. 2020) and thus may be important for driving woody plant growth by increasing water availability in the root zone (Knapp et al. 2008, Raz-Yaseef et al. 2012, Kulmatiski and Beard 2013). In contrast, in mesic biomes where potential evapotranspiration only slightly exceeds rainfall and rain events are typically large, extreme rain events are likely to be less important for driving tree growth because much of the rainfall from extreme events may be lost to run off or deep infiltration below the root zone or exceed the capacity of trees to uptake it (Knapp et al. 2008, Ye et al. 2016). However, there is very little empirical evidence of the role of extreme rain events in driving the growth of plants, particularly the growth of woody plants in shrub- or tree-dominated ecosystems across both mesic and water-limited biomes (Beier et al. 2012; but see Kulmatiski and Beard 2013, Ye et al. 2016).

Understanding growth responses of woody species to changes in the frequency or intensity of extreme rain events is important for several reasons. First, the frequency and intensity of rainfall events may be more important than the mean amount of rainfall for explaining the spatial distribution and growth of woody vegetation. For example, the encroachment of woody vegetation into African savannas has been attributed to increases in rainfall intensity rather than total rainfall (Good and Caylor 2011, Kulmatiski and Beard 2013). Second, wood is a major long-term carbon sink in terrestrial ecosystems (Pan et al. 2011); hence, understanding how wood production is influenced by variation in the frequency or intensity of rain events is critical to understanding the potential impacts of climate change on terrestrial carbon fluxes. Third, tree stem growth (i.e. ring width) is one of the primary sources of information used to understand past climate variability. Tree rings have been used to reconstruct long records of annual or seasonal rainfall amount for many environments around the world where tree growth is primarily limited by water availability. Such reconstructions have played a critical role in identifying the timescales and magnitudes of hydroclimatic variability as well as the frequency of past extreme climatic periods (Cullen and Grierson 2009, Cook et al. 2010, 2015, 2020, Palmer et al. 2015, Allen et al. 2017). However, few tree-ring studies have considered how variation in the way that rainfall is delivered – namely the frequency and intensity of rain events – influences how much of the total rainfall is available for tree use and thus contributes to growth.

Here, we use five records of annual growth (ring width) of the Australian tree conifer *Callitris columellaris* (Cupressaceae) and instrumental daily rainfall data to investigate how inter-annual variation in the intensity and frequency of rain events influences tree growth. We selected this species because it is one of the few mainland Australian tree species that produces clear growth rings that typically represent annual growth. *C. columellaris* is also widely distributed throughout mainland Australia. Our five sites span > 20° latitude and a broad climatic gradient from the tropical north of Australia to the semi-arid south of Western Australia, providing a unique opportunity to investigate whether the relationship between tree growth and rainfall varies among biomes while keeping species physiology and morphology relatively constant. *Callitris* spp. have shallow roots (the majority of roots occur in the top 50 cm; Eberbach 2003) and exhibit anisohydric stomatal control and a highly opportunistic water use strategy. Consequently, their growth is highly responsive to rainfall (Brodribb et al. 2013). Similar hydraulic traits are also observed in other Australian small tree species, including the *Acacia aneura* species complex, which dominate much of the semi-arid and arid woodlands of Australia (Page et al. 2016, Creek et al. 2018). Consequently, while we expect that *C. columellaris* can respond to smaller rain events than deep-rooted species, we use it here as an indicator of the likely response of shallow-rooted trees and shrubs to variation in the intensity and frequency of rainfall.

Given projected changes in the frequency and intensity of extreme rain events (Alexander 2015, Monier and Gao 2015, Myhre et al. 2019) and evidence of their importance for driving inter-annual variation in productivity and growth in some ecosystems (Heisler-White et al. 2009, Kulmatiski and Beard 2013, Ye et al. 2016, Post and Knapp 2020), we are particularly interested in determining whether extreme rain events are important for driving inter-annual variation in the growth of *Callitris*. Rather than arbitrarily defining a

single 'extreme' threshold, which may obscure details of other parts of the daily rainfall distribution that may be important for driving growth, we instead investigate the relationship between growth and the frequency and amount of rainfall from rain events spanning the full distribution of daily rainfall, from all rain events to the extreme upper tail (> 90th percentile) of the daily rainfall distribution. In addition, given that the importance of extreme rain events is expected to be contingent on typical rainfall regimes and thus to vary among biomes (Knapp et al. 2008), we also aim to determine if the relationship between tree growth and the intensity and frequency of rain events differs between mesic (tropical) and water-limited (semi-arid) biomes of Australia.

Material and methods

Tree growth and rainfall data

We used five ring-width chronologies of *Callitris columellaris*: three are published (LTY, Cullen and Grierson 2009; CJD, O'Donnell et al. 2015; KOR, Allen et al. 2019) and two have been recently developed (LDE and CHR). To account for potential age-related decline in ring width, we statistically detrended the raw ring-width measurements to remove age-related (non-climatic) trends and converted them to ring-width indices (RWI) as residuals from the detrending curve (Cook and Peters 1997). The LTY, LDE, CJD and CHR ring-width series were first power-transformed to stabilise variance (Cook and Peters 1997) and detrended using an age-dependent spline. The KOR ring-width chronology was used here as it was published in Allen et al. (2019). The KOR series were also power-transformed prior to detrending with a negative exponential or linear model. All series for all sites were detrended in a signal free environment (Melvin and Briffa 2008) using the RCSigFree program (<http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software>). Further details on the sample size, detrending methods and statistical quality can be found in O'Donnell et al. (2015) for the CJD chronology and Allen et al. (2019) for the KOR chronology. Details of the previously published LTY chronology (1655–2005 CE) can been found in Cullen and Grierson (2009); however, we have now extended the LTY chronology to 2013 CE. Details of the updated LTY chronology and the new LDE and CHR chronologies can be found in Supporting information).

The five sites encompass three distinct climate zones (Fig. 1). Two of the sites (KOR and CHR) are located in the seasonally dry tropics of northern Australia, with the northernmost site, KOR receiving ~1200 mm of rain per year and CHR receiving ~800 mm per year. Despite differences in the average amount of annual rainfall at KOR and CHR, the two sites have very similar daily rainfall distributions (Fig. 2) and seasonal rainfall distribution (Supporting information). The other three sites are all located in semi-arid biomes, but experience different seasonal distributions of rainfall; CJD is located in the sub-tropical semi-arid zone where rainfall is summer dominant, while LDE and LTY are located in the Mediterranean semi-arid zone where rainfall is winter dominant (Supporting information). All three semi-arid sites receive similar mean annual rainfall (~300–400 mm annual rainfall), but rain intensity (daily rainfall) at the sub-tropical CJD site is typically greater than at the Mediterranean sites (Fig. 2). For example, the median (50th percentile) and 90th percentile of daily rainfall at CJD (2 mm and 13 mm) are approximately twice that of LDE and LTY (1 mm and ~7 mm; Fig. 2, Table 2).

We obtained instrumental rainfall data from the Australian Bureau of Meteorology, (<http://www.bom.gov.au/climate/data/>). Owing to the remote locations of our sites, there were few long, high-quality instrumental records of rainfall within 50 km of the sites. Consequently, we searched for stations within a 2° × 2° area centred on each site to find between 3 and 8 stations with long (> 60 years) daily rainfall data near each site and then calculated the mean of daily rainfall across these stations to generate a regional daily rainfall dataset. Further details of the rainfall data used here can be found in Supporting information.

Rainfall variables and regression models

We used the *monthly_response()* function in the DendroTools package (Jevšenak and Levanič 2018) in R 3.6.1 (<www.r-project.org>) to calculate Pearson correlations between RWI and total rainfall for each month as well as for all periods between 3 and 12 consecutive months out of a possible 24-month window (previous calendar year and current calendar year). We determined that the growth (as RWI) of *C. columellaris* was most strongly related to total annual (12 month) rainfall at CJD and CHR and to rainfall during a shorter (< 12 month) 'growing season' at KOR, LDE and LTY (Supporting information). Consequently, we use the following seasons to define 'growing season' rainfall variables: total annual rainfall for CJD (Dec–Nov; 12 months) and CHR (Jun–May; 12 months) and autumn-winter rainfall for LDE (Feb–Aug; 7 months) and LTY (Jan–Sep; 9 months). For the wet-tropical KOR site, we included rainfall in the transitional seasons both before (Sep–Nov) and after (Mar–Jun) the main wet season in the 'growing season' (7 months total) as rainfall in both seasons is strongly related to tree growth while rainfall during the wet season months (Dec–Feb) is not (Supporting information).

We conducted several analyses to determine whether all rainfall events or only part of the daily rainfall size distribution – particularly the extreme upper tail – is responsible for driving most of the inter-annual variation in growth of *C. columellaris*. We used a flexible approach to test the hypothesis that only rain events above some threshold value drive inter-annual variation in growth. We defined *thresh* to be the minimum amount of daily rainfall required to drive growth and then considered a range of values for *thresh* between 0.1 and 30 mm. A threshold of 0.1 mm means that all rain days are counted, while a threshold of 30 mm means that only rain days with at least 30 mm rainfall are counted. We varied the

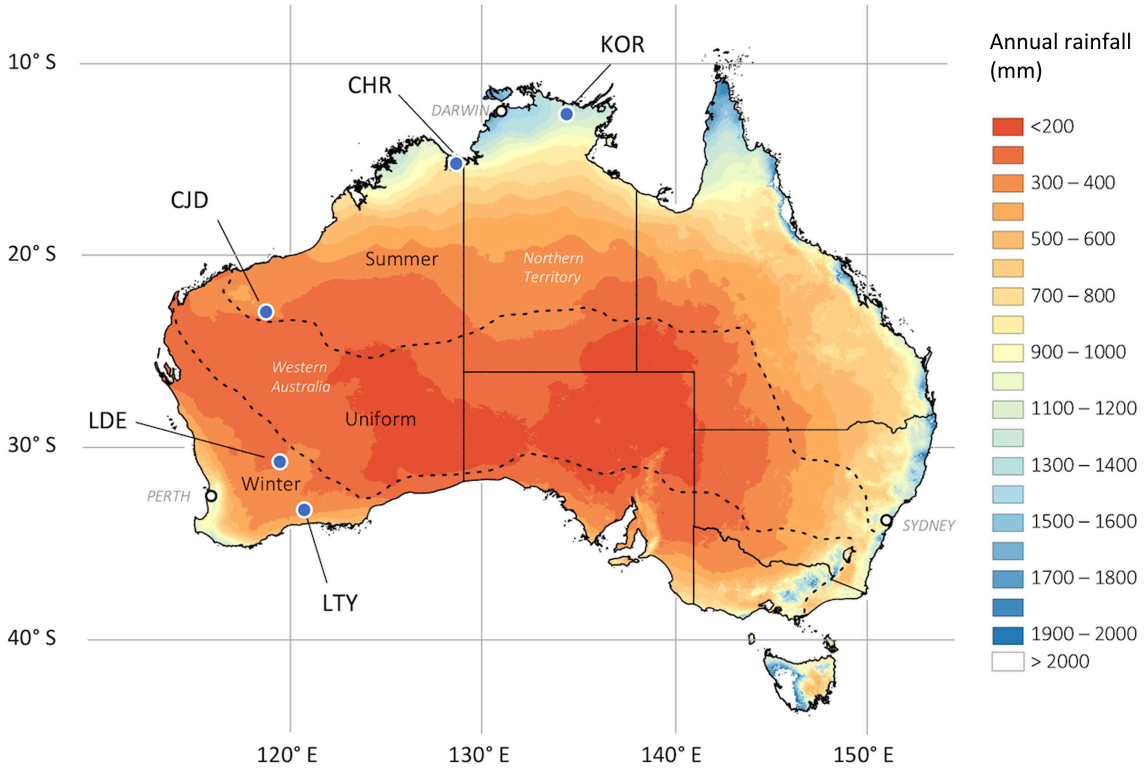

Figure 1. Location of the five *Callitris columellaris* sites in relation to annual rainfall and rainfall seasonality zones of Australia. Coloured shading indicates the 1961–1990 mean annual (January–December) rainfall amount (data sourced from the Australian Bureau of Meteorology: <http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp>). Dashed lines indicate boundaries between areas with summer-dominated, uniform (both summer and winter) or winter-dominated rainfall distributions (data sourced from the Australian Bureau of Meteorology: <http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/index.jsp?maptype=seasb#maps>). Solid black lines indicate state and territory boundaries; white dots indicate the location of some state capital cities.

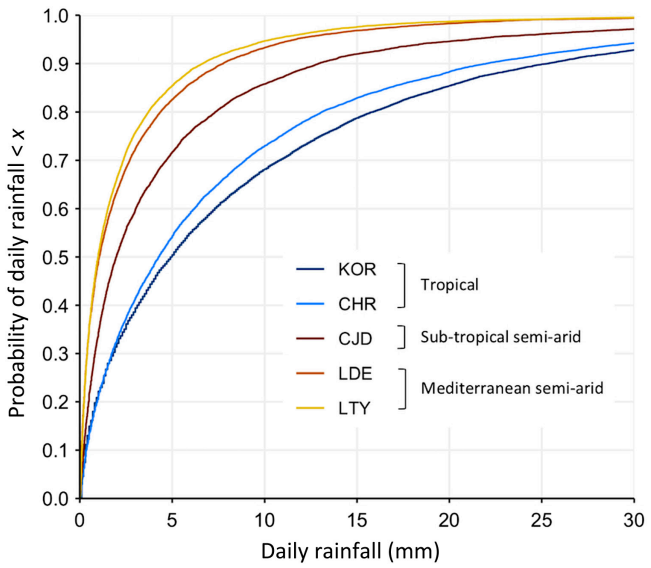

Figure 2. Empirical cumulative probability distribution of daily rainfall for each of the five study sites. Probability distributions are based on ~110 years (1908–2018 CE) of daily rainfall data. Note: The x-axis has been truncated at 30 mm; the maximum daily rainfall amount was 290 mm at CHR.

value of *thresh* from 0.1 mm to 30 mm in 0.1 mm increments (i.e. 300 possible *thresh* values). For each of the 300 possible *thresh* values, we then calculated two predictor variables for each year; the number of days in the growing season when rainfall exceeded the threshold, $Days_{>thresh}$, and the sum of rainfall from those days, $Rain_{>thresh}$. For each of the 300 possible *thresh* values, we then fitted a simple linear model with RWI as the response variable and $Days_{>thresh}$ as the predictor, using the *lm()* function in the base package of R (<www.r-project.org>). For each of the 300 possible *thresh* values, we also fitted a linear model with RWI as the response variable and $Rain_{>thresh}$ as the predictor; however, given that the relationships between *C. columellaris* growth and rainfall amount is non-linear (concave down) in the tropics (O'Donnell et al. 2021), we also tested whether quadratic polynomial models explained the relationship between RWI and $Rain_{>thresh}$ better than simple linear models at the tropical sites using F-tests (the *anova()* function in R). Quadratic polynomials showed a signficantly better fit to the RWI data at the tropical sites than simple linear models for all $Rain_{>thresh}$ values we tested (i.e. between 0.1 and 30 mm). Hence for the two tropical sites, all relationships between rainfall amount ($Rain_{>thresh}$) and growth were modelled with quadratic polynomials. For the semi-arid sites, these relationships were best described by linear models.

We plotted the resulting model R^2 for each of the 300 possible values of *thresh* for each of the two predictors ($Rain_{>thresh}$ and $Days_{>thresh}$; Fig. 3). For each site, we observed a peak in R^2 and defined the threshold value where R^2 was maximised as the 'optimal' threshold. We then called the value of $Days_{>thresh}$ at this optimal threshold (the number of days when rainfall exceeded this optimal threshold), $Days_{>optimal.thresh}$. Similarly, we called the value of $Rain_{>thresh}$ at the optimal threshold, $Rain_{>optimal.thresh}$ (Table 1). For each site and each of the two predictor variables, we then determined if the model using the optimal threshold explained 'significantly' more variance in RWI than the model without a threshold, using a conservative criterion of $\Delta R^2 > 0.02$. We compared differences in AIC and R^2 among models and also p-values from F-tests and found that for these data, our criterion for 'significance' of $\Delta R^2 > 0.02$ is more conservative than the generally accepted criterion of $\Delta AIC > 2$ or $p < 0.05$ from an F-test.

We also determined whether the number of extreme rain days ($Days_{>extreme.thresh}$) or the amount of rainfall from extreme rain days (extreme rainfall, $Rain_{>extreme.thresh}$) was a better predictor of RWI than all rain days or total rainfall (i.e. no threshold) using the same $\Delta R^2 > 0.02$ criterion. For this purpose, we defined the extreme threshold as the 90th percentile (i.e. heaviest 10%) of daily rainfall across all rain days of the entire rainfall record for each site (i.e. ~1908–2016 CE).

We note that the optimal rainfall threshold for $Days_{>optimal.thresh}$ is not necessarily the same as the optimal threshold for $Rain_{>optimal.thresh}$ at each site, and the values for both vary among sites. On the other hand, the value of the threshold used for calculating both $Days_{>extreme.thresh}$ and $Rain_{>extreme.thresh}$ is the same (the 90th percentile) within a site, but varies among sites.

Results

Rainfall amount

For the three semi-arid sites, we found stronger relationships between growth (as RWI) and rainfall amount if the smallest daily rain events were excluded from rainfall totals. For each site, a range of threshold values resulted in rainfall amount variables that were better predictors ($\Delta R^2 > 0.02$) than total rainfall (i.e. no threshold; Fig. 3). For example, at CJD, rainfall from rain days that exceed a range of thresholds between 3.0 and 12.2 mm explained > 2% more variance in RWI than total rainfall (blue shading; Fig. 3c). For each of the semi-arid sites, the optimal rainfall thresholds (maximum R^2) were between 4.7 and 6.8 mm and equivalent to the 74th to 90th percentile of daily rainfall (Table 2, Fig. 3c–e). Relationships between RWI and $Rain_{>optimal.thresh}$ at the semi-arid sites were linear (Fig. 4a) and strong ($R^2 = 0.45–0.75$; Table 2) and showed similar slopes (Fig. 4a; Supporting information).

The optimal rainfall threshold and extreme rainfall threshold (90th percentile) at LTY were almost identical (6.8 and 6.6 mm) indicating that the extreme upper tail (> 90th percentile) of the daily rainfall distribution best explains inter-annual variation in RWI (Table 2, Fig. 3e). $Rain_{>extreme.thresh}$ (> 7.8 mm) was also a significant and strong predictor of RWI at LDE, explaining as much variance as total rainfall ($R^2 = 0.59$ for both; Table 2) and showing a similar slope (Supporting information). However, $Rain_{>optimal.thresh}$ (> 4.7 mm), which represents the 81st percentile of daily rainfall was a better predictor ($R^2 = 0.61$) of RWI than extreme rainfall ($Rain_{>extreme.thresh}$, $R^2 = 0.59$; Table 2, Fig. 3d). At the sub-tropical semi-arid CJD site, the extreme rainfall threshold (12.9 mm) was more than twice the size of the optimal threshold (5.5 mm) and greater than the extreme threshold for both of the Mediterranean semi-arid sites (6.6 mm at LTY and 7.8 mm at LDE; Table 2). Despite this large difference, $Rain_{>extreme.thresh}$ at CJD was a better predictor of RWI ($R^2 = 0.73$) than total rainfall ($R^2 = 0.70$), although a weaker predictor of RWI than $Rain_{>optimal.thresh}$ ($R^2 = 0.75$; Table 2, Fig. 3c). In contrast to the two winter-rainfall dominated semi-arid sites (LDE and LTY), the proportion of variance in RWI explained by rainfall amount did not decline steeply with increasing threshold size at the summer-rainfall dominated semi-arid CJD site (Fig. 3). In fact, rainfall from > 95th percentile rain days (i.e. > 21.5 mm) at CJD was nearly as good as a predictor of RWI (i.e. $\Delta R^2 < 0.02$) as total rainfall. In addition, rainfall from the highest threshold we tested (i.e. > 30 mm), which is equivalent to the 97th percentile of daily rainfall at CJD still explained more than 62% of the variance in RWI (Fig. 3c).

In contrast to the semi-arid sites, we found that excluding the smallest events from rainfall totals (i.e. using a threshold) at the tropical sites did not substantially improve the relationship between RWI and rainfall amount (i.e. $\Delta R^2 < 0.02$; Fig. 3a–b). While optimal rainfall thresholds (highest R^2) were found, these were not better predictors of RWI than total rainfall (i.e. $\Delta R^2 < 0.02$; Table 2). However, excluding the smallest events (< 5.9 mm at CHR or < 7.3 mm at KOR) from rainfall totals did not result in a substantial loss of explanatory power compared to using total rainfall as a predictor (i.e. $\Delta R^2 < 0.02$; Fig. 3a–b). Extreme rainfall thresholds were much greater at the tropical sites than at the semi-arid sites (i.e. > 22 mm for CHR and > 25.3 mm for KOR) and $Rain_{>extreme.thresh}$ at the tropical sites was a weaker predictor of RWI than total rainfall, explaining approximately 13% less of the variance in RWI (Table 2). In the case of KOR, $Rain_{>extreme.thresh}$ also showed a more concave relationship with growth than total rainfall or $Rain_{>optimal.thresh}$ (Supporting information).

Number of rain days

Across both semi-arid and tropical climate zones, relationships between RWI and the number of all rain days (> 0 mm) were typically quite weak ($R^2 < 0.23$; Table 3). However, applying thresholds of 0.4 mm or more (up to ~22 mm for LTY, CHR and KOR, > 30 mm for LDE and CJD) to define the number of rain days improved the variance in RWI explained (i.e. $\Delta R^2 > 0.02$; Fig. 3). At the semi-arid sites, the optimal rain day thresholds (i.e. 7.8–20.1

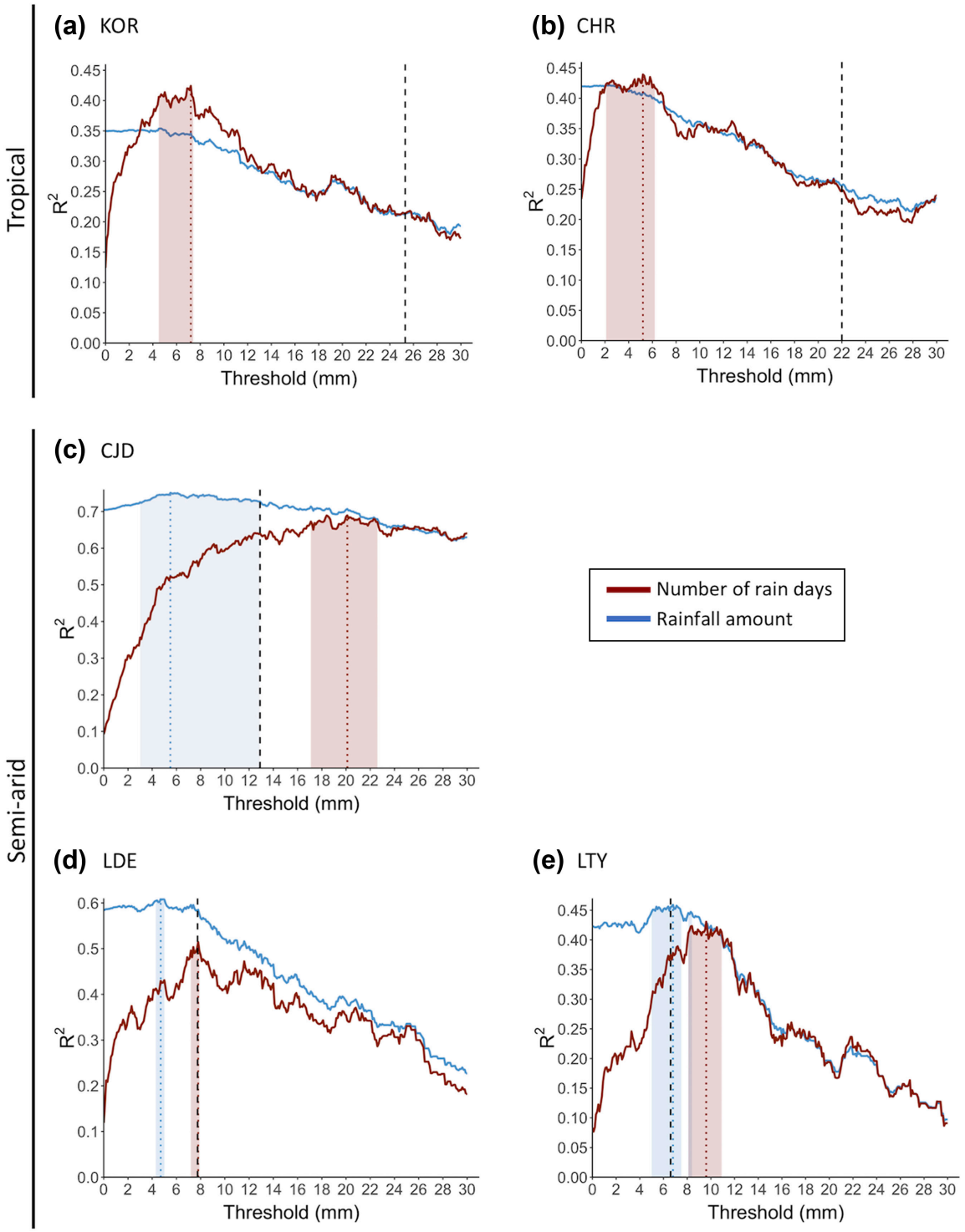

Figure 3. Proportion of variance in ring-width index (RWI) of *Callitris columellaris* explained (R^2) by the amount of rainfall (blue) or the number of rain days (red) during the growing season that exceed a threshold between 0 mm (all rainfall/all rain days) and 30 mm. Vertical dotted lines indicate the optimal thresholds (highest R^2) for rainfall amount ($Rain_{>optimal.thresh}$; blue) and the number of rain days ($Days_{>optimal.thresh}$; red) during the growing season. Shaded blue vertical bands indicate the range of threshold values for rainfall amount that are considered better predictors ($\Delta R^2 > 0.02$) of RWI than total rainfall (0 mm threshold). Shaded red vertical bands indicate the range of threshold values for the number of rain days that produce R^2 values within 0.02 of the optimal threshold. Vertical dashed black lines indicate the 90th percentile of daily rainfall at each site.

Table 1. Definitions of predictor variables used to examine the relationship between rainfall and growth (RWI) of *Callitris columellaris*.

Variable name	Definition	Unit
Total rainfall	Total amount of growing season rainfall from all rain days (> 0 mm)	mm
All rain days	The number of days during the growing season with rainfall (> 0 mm)	days
$Rain_{>optimal.thresh}$	Total amount of growing season rainfall from rain days that exceed the threshold amount that best explains variance in RWI (highest R^2)	mm
$Days_{>optimal.thresh}$	The number of days during the growing season with rainfall that exceeds the threshold amount that best explains variance in RWI (highest R^2)	days
$Rain_{>extreme.thresh}$	Total amount of growing season rainfall from rain days that exceed the 90th percentile of daily rainfall	mm
$Days_{>extreme.thresh}$	The number of days during the growing season with rainfall that exceeds the 90th percentile of daily rainfall	days

mm) represented extreme rain days (i.e. 90–95th percentile, Table 3). Both $Days_{>optimal.thresh}$ and $Days_{>extreme.thresh}$ were better predictors of RWI than the number of all rain days at the semi-arid sites, improving the variance explained by 25–60% (Table 3, Fig. 3c–e; Supporting information). While $Days_{>optimal.thresh}$ or $Days_{>extreme.thresh}$ were strong predictors of RWI at the semi-arid arid sites, they were less important than any measure of rainfall amount (total, $Rain_{>optimal.thresh}$ or $Rain_{>extreme.thresh}$; Table 2, 3, Fig. 3c–e).

The optimal thresholds for the number of rain days at the tropical sites represented only the ~55–60th percentile of daily rainfall (Table 3). $Days_{>optimal.thresh}$ at the tropical sites was a better predictor of RWI than the number of all rain days or $Days_{>extreme.thresh}$, explaining ~20% more variance in RWI (Table 3). In contrast to the semi-arid sites, the number of $Days_{>optimal.thresh}$ was either as good or a better predictor of RWI than any measure of rainfall amount (Fig. 3a–b, Table 2, 3).

Discussion

Extreme rain events are particularly important for driving tree growth in semi-arid Australia, where we found that the heaviest 10–25% of rain days explain the most inter-annual variation in growth of *Callitris columellaris*. This finding is consistent with other studies in water-limited biomes, which show that variation in the intensity and frequency of extreme rain events is more important than total rainfall for driving tree growth (Kulmatiski and Beard 2013) or ecosystem productivity (Heisler-White et al. 2008, 2009, Ye et al. 2016). Our finding that smaller rain events (< ~5 mm; Table 2) contribute proportionately less or perhaps not at all to growth than larger events in semi-arid Australia is also consistent with the concept of 'effective' or 'biologically important' rainfall in semi-arid and arid systems, where a minimum threshold of rainfall is required to stimulate plant productivity and growth (Noy-Meir 1973, Ogle and Reynolds 2004, Schwinning and Sala 2004). Small rain events, particularly temporally isolated events, are unlikely to penetrate far into the soil profile in water-limited environments because much of the rainfall is either intercepted (by the canopy and litter) or lost to evaporation. Instead, larger events are generally required to infiltrate soil to a depth where it becomes plant-available and can trigger assimilation processes (Huxman et al. 2004, Reynolds et al. 2004, Knapp et al. 2008, Raz-Yaseef et al. 2012, Kulmatiski and Beard 2013).

Several empirical studies support the concept of 'effective' rain events in semi-arid and arid environments, reporting measurable physiological responses (i.e. increases in water use and/or gas exchange) of shallow-rooted shrubs or trees (Burgess 2006, Zeppel et al. 2008, Zhao and Liu 2010, Eamus et al. 2013) or increases in ecosystem productivity (Li et al. 2015, Fan et al. 2016) typically only following larger rain events. For example, Burgess (2006) found that rain events < 4 mm in semi-arid southwest Australia (i.e. the same climate zone as our LTY and LDE sites) did not generate a sap flow response in a suite of shrubs and trees, including another *Callitris* species (*C. arenaria*, previously known as

Table 2. Proportion of variance in RWI of *Callitris columellaris* explained by the amount of rainfall (total, $Rain_{>optimal.thresh}$ or $Rain_{>extreme.thresh}$) during the 'growing season'.

		Total rainfall	$Rain_{>optimal.thresh}$				$Rain_{>extreme.thresh}$			
	Site	R^2	Thresh (mm)	Thresh (PCTL)	Annual rain (%)	R^2	Thresh (mm)	Annual rain (%)	R^2	Season (no. months)
Tropical	KOR	**0.350**	4.7	49.0	91.5	**0.354**	25.3	41.6	0.212	Sep–Nov + Mar–Jun (7)
	CHR	**0.432**	2.1	33.8	96.3	**0.434**	22.0	41.3	0.261	Jun–May (12)
Semi-arid	CJD	0.704	5.5	74.2	74.4	**0.751**	12.9	47.6	0.727	Dec–Nov (12)
	LDE	0.584	4.7	81.5	64.8	**0.609**	7.8	48.2	0.585	Feb–Aug (7)
	LTY	0.423	6.8	90.3	48.1	**0.459**	6.6	49.2	0.455	Jan–Sep (9)

Bold values indicate the variable(s) that showed the greatest predictive skill (i.e. R^2 > 0.02 greater than other models) within each site (i.e. within rows). KOR and CHR were fitted with quadratic polynomial models. CJD, LDE and LTY were fitted with simple linear models. All variables were significant predictors of RWI at $\alpha = 0.001$. Thresh = Threshold, PCTL = Percentile, the percentage of rain days (> 0 mm) with rainfall less than the optimal threshold in the full time series of rain data for each site. % annual rainfall is the long-term average (~1908–2016) percentage of annual rainfall that falls as part of rain days with rainfall greater than the threshold (optimal or 90th percentile).

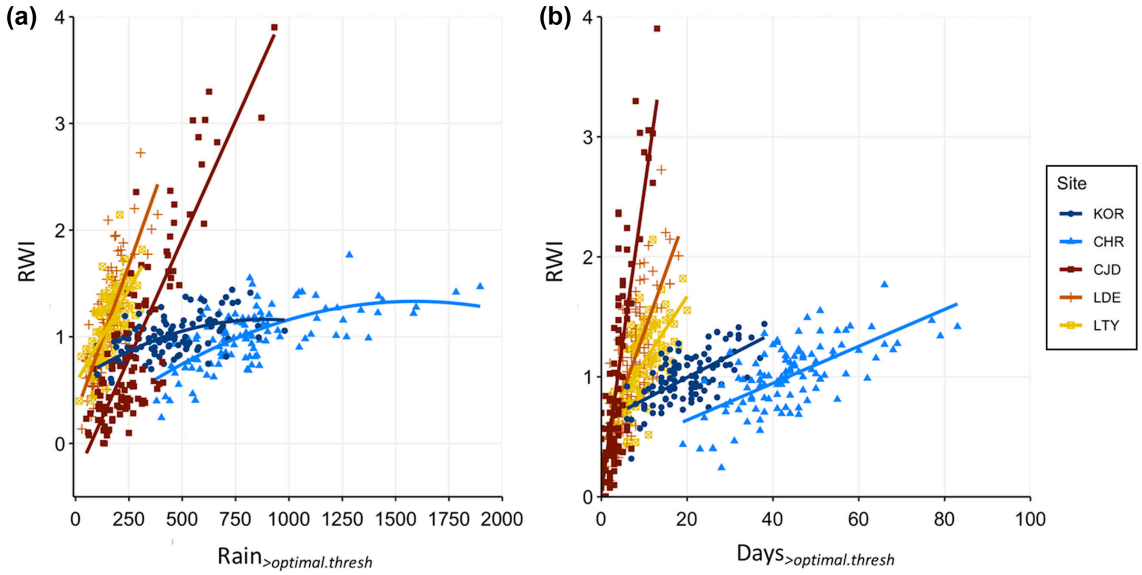

Figure 4. Relationships between ring-width index (RWI) of *Callitris columellaris* and (a) amount of rainfall from days with rainfall > optimal threshold ($Rain_{>optimal.thresh}$) and (b) the number of rain days > optimal threshold ($Days_{>optimal.thresh}$) during the growing season at tropical (blue) and semi-arid (yellow-red) sites. Lines represent fitted models. In (a) CJD, LDE and LTY are fitted with simple linear models, KOR and CHR are fitted with quadratic polynomial models. In (b) all sites are fitted with simple linear models. See Table 2 and 3 for optimal threshold values and Supporting information for the model parameter estimates and standard errors for each model.

Actinostrobus arenarius). Our findings provide evidence that the concept of 'effective' rain events also applies to the growth of shallow rooted trees in water-limited ecosystems and suggest that the threshold-responses that have been widely documented in immediate physiological processes (water use and gas exchange) of woody plants are carried over into the process of wood production.

Extreme rainfall was not as important for driving tree growth in the tropical north of Australia, where total rainfall (from all rain events) explained much more (> 13 %) of the variance in growth than extreme rainfall. However, rainfall from the smallest (< ~50th percentile) events was also not particularly important for explaining variation in growth of *Callitris* in the tropics (i.e. excluding events < 5.9 mm for CHR or < 7.3 mm for KOR did not substantially reduce the explained variance; i.e. $\Delta R^2 < 0.02$, Fig. 3a–b). In contrast, the relationship between RWI and the *number* of rain days ($Days_{>thresh}$) in the tropics was greatly improved (by > 20%) if the smallest rain events were excluded (Fig. 3, Table 3). While we found optimal thresholds for $Days_{>thresh}$ (of 5.2 mm for CHR and 7.2 mm for KOR) that explained the most variance in RWI at each tropical site, a range of thresholds between ~4.5 and 6 mm at both sites (specifically between 2.1 and 6 mm for CHR and between 4.5 and 7.4 mm for KOR) were considered as good predictors of RWI as the optimal threshold (i.e. R^2 within 0.02 of the optimal threshold; Fig. 3). Previously, Cook and Heerdegen (2001) noted that the mean daily potential evaporation during the wet season in the Australian tropics was > ~5 mm and they consequently defined 'rain days' for this region as days when rainfall exceeded 5 mm (i.e. rainfall exceeded potential evaporation). Our findings are consistent with the definition of 'rain days' used by Cook and Heerdegen (2001) and provide further support for the use of a threshold of ~5 mm to define rain days that are important for tree growth in tropical northern Australia.

Our results suggest that the relative importance (ΔR^2) of the *number* of rain days > optimal threshold ($days_{>optimal.thresh}$)

Table 3. Proportion of variance in RWI of *Callitris columellaris* explained by the number of rain days (all, $Days_{>optimal.thresh}$ or $Days_{>extreme.thresh}$) during the 'growing season'.

		All rain days	$Days_{>optimal.thresh}$			$Days_{>extreme.thresh}$		
	Site	R^2	Threshold (mm)	PCTL	R^2	Threshold (mm)	R^2	Season (no. months)
Tropical	KOR	0.124	7.2	59.7	**0.424**	25.3	0.214	Sep–Nov + Mar–Jun (7)
	CHR	0.234	5.2	55.6	**0.439**	22.0	0.246	Jun–May (12)
Semi-arid	CJD	0.092	20.1	94.6	**0.690**	12.9	0.640	Dec–Nov (12)
	LDE	0.119	7.8	90.0	**0.515**	7.8	**0.515**	Feb–Aug (7)
	LTY	0.083	9.6	94.3	**0.431**	6.6	0.375	Jan–Sep (9)

Bold values indicate the variable(s) that showed the greatest predictive skill (i.e. $R^2 > 0.02$ greater than other models) within each site (i.e. within rows). All models were simple linear regression models. PCTL = percentile; the percentage of rain days with rainfall less than the optimal threshold in the full time series of rain data for each site.

versus the total *amount* of rainfall for driving growth may be greater in biomes with higher mean annual rainfall (Table 3). At the wettest tropical site (i.e. KOR, ~1200 mm annual rainfall), the number of $Days_{>optimal.thresh}$ (> 7.2 mm) during the growing season was a stronger predictor of *Callitris columellaris* growth than total rainfall amount. Allen et al. (2019) also found that the growth of *Callitris columellaris* at KOR and another site in a higher rainfall zone of the Australian tropics (> 1500 mm) was more strongly related to the number of rain days > 5 mm than the total amount of rainfall. However, at the tropical site with lower rainfall (CHR; ~800 mm annual rainfall), the number of $Days_{>optimal.thresh}$ (> 5.2 mm) and total rainfall during the growing season explained similar proportions of variance in growth. There are a few possible explanations for the stronger relationship between *Callitris columellaris* growth and $Days_{>optimal.thresh}$ than rainfall amount at the higher rainfall end of the Australian tropics. First, much of the rainfall in the tropics occurs as part of extreme rain events (i.e. > 41% of annual rainfall is from > 25 mm rain days at KOR; Table 2). It is likely that much of the rainfall from extreme rain events is not used by shallow rooted trees, either because it exceeds the capacity of the trees to uptake and use it (as growth may become more limited by light or nutrient availability), or because much of it is lost to runoff or deeper into the soil profile below rooting depth (Mott 1974, Cook and Heerdegen 2001). Drew et al. (2014) observed that the size of stem increments of *Callitris columellaris* in tropical northern Australia (> 1700 mm) was not consistently related to the size of rain events. In particular, Drew et al. (2014) concluded that larger rain events did not consistently lead to larger stem increments. Hence, while a large proportion of rainfall is delivered in extreme events in the wet tropics, extreme rain events likely contribute proportionately less to growth than they do to rainfall totals, resulting in weaker relationships between rainfall amount and growth. Second, the number of $Days_{>optimal.thresh}$ may provide a better indication of the relative opportunity for growth (i.e. the occurrence of favourable conditions for growth) than rainfall amount. Even in years with high rainfall, tree growth may be limited by water-availability at times if rainfall is distributed into fewer, but higher-intensity rainfall events resulting in more frequent or longer dry intervals between rain events (Knapp et al. 2008, Ye et al. 2016).

Potential impacts of intensification of rainfall regimes on growth

Climate models predict an increase in the intensity of extreme rain events across both the tropical zone of northern Australia and the semi-arid zone of western Australia (CSIRO 2015). Our results from tropical Australia are consistent with empirical studies of productivity in other mesic ecosystems (Fay et al. 2008, Manea and Leishman 2018, Padilla et al. 2019, Felton et al. 2020) and suggest that an increase in the intensity of rain events in the Australian tropics could potentially have a negative impact on tree growth if the redistribution of rainfall into fewer, larger events results in longer dry periods in between rain events and/or a greater proportional loss of rainfall to runoff or infiltration deep into the soil profile (Knapp et al. 2008, Ye et al. 2016). Our findings for semi-arid biomes of Australia are consistent with empirical studies in other water-limited ecosystems, which show increased tree growth (Kulmatiski and Beard 2013) or ecosystem productivity (Heisler-White et al. 2008, 2009) in response to an increase in the relative contribution of rainfall from extreme events. Thus, in contrast to mesic biomes, an increase in the intensity of extreme rainfall events in water-limited biomes (e.g. semi-arid Australia) is likely to have significant and positive impacts on tree growth, by increasing soil water availability and infiltration to the rooting zone. Such an effect has been observed in Kruger National Park, South Africa, where an artificial shift to fewer, more intense rain events resulted in deeper infiltration and favoured the growth of woody plants over grasses (Kulmatiski and Beard 2013). However, in the semi-arid southwest of Australia, where the LTY and LDE sites are located, in addition to an increase in the intensity of rainfall events, climate models predict a decline in winter (growing season) rainfall amount in the future (CSIRO 2015). While the degree to which the intensity of rain events in semi-arid southwest Australia will change versus the amount of growing season rainfall remains uncertain (CSIRO 2015), our findings suggest that the positive effect of an increase in the intensity of rain events on the growth of shallow-rooted trees and shrubs may at least partially counteract the negative effect of an overall reduction in growing season rainfall.

Implications for dendroclimatology and its application

Our target species, *Callitris columellaris*, is commonly used in Australian dendroclimatological research (Cullen and Grierson 2007, 2009, Baker et al. 2008, D'Arrigo et al. 2008, Sgherza et al. 2010, O'Donnell et al. 2015, 2018, Allen et al. 2019). Hence, understanding how the intra-annual distribution of rainfall, not just total amount, influences their growth is important for interpreting past climatic variability from their growth rings. Our findings here and previously (O'Donnell et al. 2021) show that the relationship between growth of *C. columellaris* and rainfall amount in the tropics is of a non-linear concave down form, where reductions in growth in dry years are greater than increases in growth in wet years (Dannenberg et al. 2019, Gherardi and Sala 2019). Thus, ring widths of *C. columellaris* in the tropics exhibit asymmetry in the recording of extreme years – they record extreme dry years more accurately than extreme wet years. Consequently, tree-ring records from the Australian tropics may be useful as indicators of particularly dry years, but are less useful for distinguishing between years of average or high rainfall (Drew et al. 2014). Similarly, Wise and Dannenberg (2019) found that asymmetric capture of extreme events was common in tree-ring records from the western United States, where a third of tree-ring records captured dry but not wet extremes.

Interestingly, our findings suggest that tropical *C. columellaris* tree-ring records are more suited to reconstructing the occurrence of rain days > ~5 mm (optimal threshold) than rainfall amount. While the number of rain days is not a common target for reconstruction (but see Woodhouse and Meko 1997), a reconstruction of the number of > ~5 mm rain days may be more meaningful than total rainfall for interpreting past variability in hydroclimate that is important to plant productivity and growth in the tropics and is worth further investigation.

Tree growth at the semi-arid sites exhibit strong and linear relationships with total rainfall amount; relationships that have already been used to interpret past variability of rainfall in northwest and southwest Australia (Cullen and Grierson 2009, O'Donnell et al. 2015). Our findings suggest that these records are more suited to reconstructing 'biologically important' (i.e. > optimal threshold) rainfall than total rainfall and can therefore help to better understand the timescales and magnitudes of variation in the portion of rainfall that is important for plant productivity and growth. Our findings also indicate that tree-ring width records from semi-arid Australia, where relationships with extreme rainfall and the number of extreme rain days were strong and where extreme rainfall contributes a large proportion of annual and growing season rainfall (Table 2; Lavender and Abbs 2013), could be used to understand past variability of extreme rainfall or the frequency of extreme rain events. Such potential for using tree-ring records to reconstruct extreme rainfall events has been demonstrated in the southwestern United States (Steinschneider et al. 2018). There is particularly strong potential for developing a reconstruction of extreme rainfall events in the sub-tropical, semi-arid biomes of northwest Australia, where the relationship between *C. columellaris* growth and the amount of extreme rainfall or the number of extreme rain events is very strong. Even if we had used a more conservative definition of 'extreme', these relationships remain strong; for example, using a definition of > 97th percentile (> 30 mm) for extreme rain days, extreme rainfall explains more than 60% of the variance in growth (Fig. 3). The potential to use tree-ring records from semi-arid Australia to better understand past variability of the occurrence of extreme events is particularly important given the high level of uncertainty surrounding extreme climate risk.

Conclusions

The ecological impacts of changes in the frequency and intensity of rainfall have been of increasing interest in the last decade (Knapp et al. 2008, Kulmatiski and Beard 2013, Manea and Leishman 2018, Padilla et al. 2019, Felton et al. 2020), but are still poorly resolved compared to some other aspects of global change. Our study provides important empirical evidence of the role of rain intensity and frequency in driving tree growth and provides new insights into how projected changes in rainfall regimes may impact tree growth across different biomes. Our findings indicate that projected intensification of rainfall regimes is likely to drive contrasting growth responses in mesic and water-limited biomes of Australia; potentially leading to declines in growth in mesic tropical biomes and increases in growth in water-limited semi-arid biomes. However, our findings are based on a single, shallow-rooted tree species, which we use as an indicator species. The growth response of our target species, *C. columellaris*, is likely representative of some other widespread small Australian tree species that exhibit similar hydraulic traits such as the *Acacia aneura* complex of species. However, further research is needed to determine whether the growth responses we observed for *C. columellaris* can be used to predict the growth responses of other shallow-rooted woody species, and in particular, whether the growth responses of deep-rooted woody species are likely to differ from those of shallow-rooted species. Our findings also indicate that growth rings of *C. columellaris* in water-limited biomes may provide a new avenue to reconstruct and better understand past variability of extreme rain events over multi-centennial timescales. This information is critical for placing recent and projected future changes in the frequency and intensity of extreme rain events in a long-term context and for better predicting the ecosystem impacts of such changes.

Acknowledgements – We are grateful to Ian Radford and Lachlan McCaw from the Western Australian Department of Biodiversity, Conservation and Attractions as well as Douglas Ford, Hannah Etchells, Joshua Oliver from The University of Western Australia for their assistance in collecting samples for the CHR and LDE chronologies.
Funding – This work was funded by Australian Research Council Discovery Grant DP170101033. K. Allen was supported by an Australian Research Council Discovery Grant DP0878744.
Conflicts of interest – The authors have no conflicts of interest to declare that are relevant to the content of this article.
Permits – Samples were collected with permission from the Western Australian Department of Biodiversity, Conservation and Attractions under flora collection license SW019556 issued to A. O'Donnell.

Author contributions

Alison O'Donnell: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Michael Renton**: Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Kathryn Allen**: Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Pauline Grierson**: Data curation (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.05671.

Data availability statement

The three unpublished ring width chronologies (LTY, LDE and CHR) have been uploaded to Dryad Digital Repository: <http:// dx.doi.org/10.5061/dryad.kkwh70s4d> O'Donnell et al. 2021. The CJD and KOR ring width chronologies are available from the International Tree Ring Data Bank: AUSL037 (https://www.ncdc.noaa.gov/paleo/study/18957) and AUSL054 (https://www.ncdc.noaa.gov/paleo/study/27375).

References

Alexander, L. V. 2015. Global observed long-term changes in temperature and precipitation extremes: a review of progress and limitations in IPCC assessments and beyond. – Weather Clim. Extrem. 11: 4–16.

Allen, K. J. et al. 2017. A 277 year cool season dam inflow reconstruction for Tasmania, southeastern Australia. – Water Resour. Res. 53: 400–414.

Allen, K. J. et al. 2019. Two climate-sensitive tree-ring chronologies from Arnhem Land, monsoonal Australia. – Austral Ecol. 44: 581–596.

Baker, P. J. et al. 2008. The dendrochronology of *Callitris intratropica* in northern Australia: annual ring structure, chronology development and climate correlations. – Aust. J. Bot. 56: 311–320.

Beier, C. et al. 2012. Precipitation manipulation experiments – challenges and recommendations for the future. – Ecol. Lett. 15: 899–911.

Brodribb, T. J. et al. 2013. Conservative water management in the widespread conifer genus *Callitris*. – AoB Plants 5: plt052.

Burgess, S. S. O. 2006. Measuring transpiration responses to summer precipitation in a Mediterranean climate: a simple screening tool for identifying plant water-use strategies. – Physiol. Plant. 127: 404–412.

Cook, E. R. and Peters, K. 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. – Holocene 7: 361–370.

Cook, E. R. et al. 2010. Asian monsoon failure and megadrought during the last millennium. – Science 328: 486–489.

Cook, E. R. et al. 2015. Old world megadroughts and pluvials during the common era. – Sci. Adv. 1: 1–10.

Cook, E. R. et al. 2020. The European Russia Drought Atlas (1400–2016 CE). – Clim. Dyn. 54: 2317–2335.

Cook, G. D. and Heerdegen, R. G. 2001. Spatial variation in the duration of the rainy season in monsoonal Australia. – Int. J. Climatol. 21: 1723–1732.

Creek, D. et al. 2018. Coordination between leaf, stem and root hydraulics and gas exchange in three arid-zone angiosperms during severe drought and recovery. – Plant Cell Environ. 41: 2869–2881.

CSIRO 2015. Climate Change in Australia – projections for Australia's NRM regions. – <https://www.climatechangeinaustralia.gov.au/en/impacts-and-adaptation/nrm-regions/>.

Cullen, L. E. and Grierson, P. F. 2007. A stable oxygen, but not carbon, isotope chronology of *Callitris columellaris* reflects recent climate change in north-western Australia. – Clim. Change 85: 213–229.

Cullen, L. E. and Grierson, P. F. 2009. Multi-decadal scale variability in autumn-winter rainfall in south-western Australia since 1655 AD as reconstructed from tree rings of *Callitris columellaris* (Cupressaceae). – Clim. Dyn. 33: 433–444.

D'Arrigo, R. et al. 2008. Experimental reconstruction of monsoon drought variability for Australasia using tree rings and corals. – Geophys. Res. Lett. 35: L12709.

Dannenberg, M. P. et al. 2019. Reduced tree growth in the semiarid United States due to asymmetric responses to intensifying precipitation extremes. – Sci. Adv. 5: 1–11.

Donat, M. G. et al. 2016. More extreme precipitation in the world's dry and wet regions. – Nat. Clim. Change 6: 508–513.

Drew, D. M. et al. 2014. The number of days on which increment occurs is the primary determinant of annual ring width in *Callitris intratropica*. – TREES Struct. Funct. 28: 31–40.

Eamus, D. et al. 2013. Carbon and water fluxes in an arid-zone acacia savanna woodland: an analyses of seasonal patterns and responses to rainfall events. – Agric. For. Meteorol. 182–183: 225–238.

Eberbach, P. L. 2003. The eco-hydrology of partly cleared, native ecosystems in southern Australia: a review. – Plant Soil 257: 357–369.

Fan, Y. et al. 2016. Divergent responses of vegetation aboveground net primary productivity to rainfall pulses in the Inner Mongolian Plateau, China. – J. Arid Environ. 129: 1–8.

Fay, P. A. et al. 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. – Global Change Biol. 14: 1600–1608.

Felton, A. J. et al. 2020. Precipitation amount and event size interact to reduce ecosystem functioning during dry years in a mesic grassland. – Global Change Biol. 26: 658–668.

Gerten, D. et al. 2008. Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. – Global Change Biol. 14: 2365–2379.

Gherardi, L. A. and Sala, O. E. 2019. Effect of interannual precipitation variability on dryland productivity: a global synthesis. – Global Change Biol. 25: 269–276.

Good, S. P. and Caylor, K. K. 2011. Climatological determinants of woody cover in Africa. – Proc. Natl Acad. Sci. USA 108: 4902–4907.

Good, S. P. et al. 2016. Global patterns of the contributions of storm frequency, intensity and seasonality to interannual variability of precipitation. – J. Clim. 29: 3–15.

Guan, K. et al. 2014. Continental-scale impacts of intra-seasonal rainfall variability on simulated ecosystem responses in Africa. – Biogeosciences 11: 6939–6954.

Heisler-White, J. L. et al. 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. – Oecologia 158: 129–140.

Heisler-White, J. L. et al. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. – Global Change Biol. 15: 2894–2904.

Huxman, T. E. et al. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. – Oecologia 141: 254–268.

IPCC 2013. Climate change 2013: the physical science basis. – In: Stocker, T. F. et al. (eds), Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press, Cambridge, UK and New York, NY, USA.

Jevšenak, J. and Levanič, T. 2018. dendroTools: R package for studying linear and nonlinear responses between tree-rings and daily environmental data. – Dendrochronologia 48: 32–39.

Knapp, A. K. et al. 2002. Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. – Science 298: 2202–2205.

Knapp, A. K. et al. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. – Bioscience 58: 811–821.
Kulmatiski, A. and Beard, K. H. 2013. Woody plant encroachment facilitated by increased precipitation intensity. – Nat. Clim. Change 3: 833–837.
Lavender, S. L. and Abbs, D. J. 2013. Trends in Australian rainfall: contribution of tropical cyclones and closed lows. – Clim. Dyn. 40: 317–326.
Li, F. et al. 2015. Productivity responses of desert vegetation to precipitation patterns across a rainfall gradient. – J. Plant Res. 128: 283–294.
Mallakpour, I. and Villarini, G. 2017. Analysis of changes in the magnitude, frequency and seasonality of heavy precipitation over the contiguous USA. – Theor. Appl. Climatol. 130: 345–363.
Manea, A. and Leishman, M. R. 2018. Soil water content variability drives productivity responses of a model grassland system to extreme rainfall events under elevated CO2. – Plant Ecol. 219: 1413–1421.
Melvin, T. M. and Briffa, K. R. 2008. A 'signal-free' approach to dendroclimatic standardisation. – Dendrochronologia 26: 71–86.
Monier, E. and Gao, X. 2015. Climate change impacts on extreme events in the United States: an uncertainty analysis. – Clim. Change 131: 67–81.
Mott, J. J. 1974. Factors affecting seed germination in three annual species from an arid region of Western Australia. – J. Ecol. 62: 699–709.
Myhre, G. et al. 2019. Frequency of extreme precipitation increases extensively with event rareness under global warming. – Sci. Rep. 9: 2–11.
Noy-Meir, I. 1973. Desert ecosystems: environment and producers. – Annu. Rev. Ecol. Syst. 4: 25–52.
O'Donnell, A. J. et al. 2015. Tree rings show recent high summer-autumn precipitation in northwest Australia is unprecedented within the last two centuries. – PLoS One 10: e0128533.
O'Donnell, A. J. et al. 2018. Potential for tree rings to reveal spatial patterns of past drought variability across western Australia. – Environ. Res. Lett. 13: 024020.
O'Donnell, A. J. et al. 2021. Data from: The role of extreme rain events in driving tree growth across a continental-scale climatic range in Australia. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.kkwh70s4d>.
O'Donnell, A. J. et al. 2021. Tree growth responses to temporal variation in rainfall differ across a continental-scale climatic gradient. – Plos One in press.
Ogle, K. and Reynolds, J. F. 2004. Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses, thresholds and delays. – Oecologia 141: 282–294.
Padilla, F. M. et al. 2019. Effects of extreme rainfall events are independent of plant species richness in an experimental grassland community. – Oecologia 191: 177–190.
Page, G. F. M. et al. 2016. Inter-specific differences in the dynamics of water use and pulse-response of co-dominant canopy species in a dryland woodland. – J. Arid Environ. 124: 332–340.
Palmer, J. G. et al. 2015. Drought variability in the eastern Australia and New Zealand summer drought atlas (ANZDA, CE 1500–2012) modulated by the Interdecadal Pacific Oscillation. – Environ. Res. Lett. 10: 124002.
Pan, Y. et al. 2011. A large and persistent carbon sink in the world's forests. – Science 333: 988–993.
Post, A. K. and Knapp, A. K. 2020. The importance of extreme rainfall events and their timing in a semi-arid grassland. – J. Ecol. 108: 2431–2443.
Raz-Yaseef, N. et al. 2012. Dynamics of evapotranspiration partitioning in a semi-arid forest as affected by temporal rainfall patterns. – Agricult. For. Meteorol. 157: 77–85.
Reyer, C. P. O. et al. 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. – Global Change Biol. 19: 75–89.
Reynolds, J. F. et al. 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water and plant responses. – Oecologia 141: 194–210.
Schwinning, S. and Sala, O. E. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. – Oecologia 141: 211–220.
Sgherza, C. et al. 2010. Climate relationships with tree-ring width and δ13C of three *Callitris* species from semiarid woodlands in south-western Australia. – Aust. J. Bot. 58: 175–187.
Steinschneider, S. et al. 2018. A 500-year tree ring-based reconstruction of extreme cold-season precipitation and number of atmospheric river landfalls across the southwestern United States. – Geophys. Res. Lett. 45: 5672–5680.
Tugwell-Wootton, T. et al. 2020. Soil moisture evaporative losses in response to wet-dry cycles in a semiarid climate. – J. Hydrol. 590: 125533.
Wise, E. K. and Dannenberg, M. P. 2019. Climate factors leading to asymmetric extreme capture in the tree-ring record. – Geophys. Res. Lett. 46: 3408–3416.
Woodhouse, C. A. and Meko, D. 1997. Number of winter precipitation days reconstructed from southwestern tree rings. – J. Clim. 10: 2663–2669.
Ye, J. S. et al. 2016. Hydrological and ecological responses of ecosystems to extreme precipitation regimes: a test of empirical-based hypotheses with an ecosystem model. – Perspect. Plant Ecol. Evol. Syst. 22: 36–46.
Zeppel, M. et al. 2008. The response of sap flow to pulses of rain in a temperate Australian woodland. – Plant Soil 305: 121–130.
Zeppel, M. J. B. et al. 2014. Impacts of extreme precipitation and seasonal changes in precipitation on plants. – Biogeosciences 11: 3083–3093.
Zhao, W. and Liu, B. 2010. The response of sap flow in shrubs to rainfall pulses in the desert region of China. – Agricult. For. Meteorol. 150: 1297–1306.